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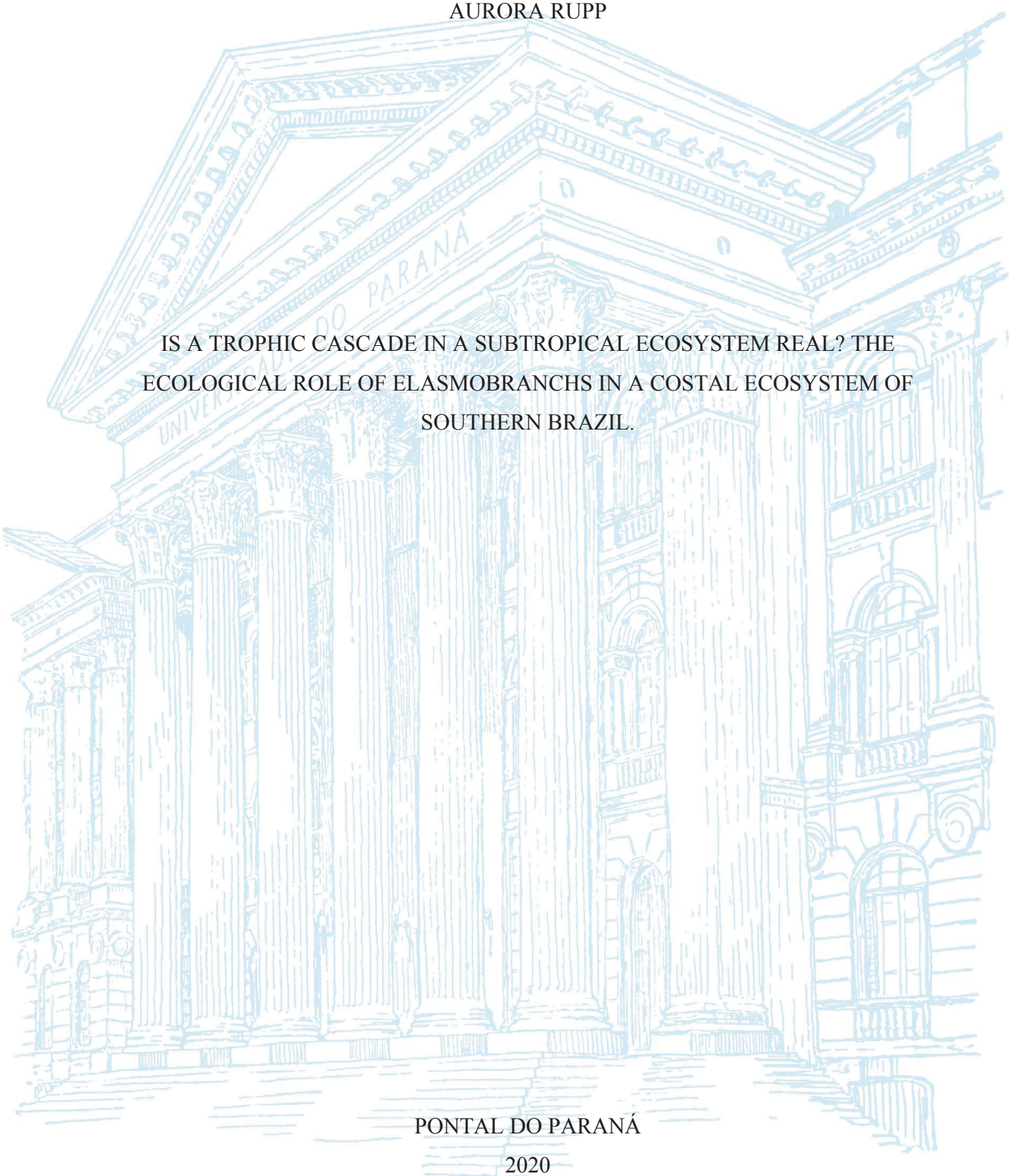

IS A TROPHIC CASCADE IN A SUBTROPICAL ECOSYSTEM REAL? THE ECOLOGICAL ROLE OF ELASMOBRANCHS IN A COSTAL ECOSYSTEM OF SOUTHERN BRAZIL.

PONTAL DO PARANÁ

2020

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IS A TROPHIC CASCADE IN A SUBTROPICAL ECOSYSTEM REAL? THE ECOLOGICAL ROLE OF ELASMOBRANCHS IN A COSTAL ECOSYSTEM OF SOUTHERN BRAZIL.

Dissertação apresentada como requisito parcial à obtenção do título de Mestre em Sistemas Costeiros e Oceânicos, no Curso de Pós-Graduação em Sistemas Costeiros e Oceânicos do Centro de Estudos do Mar, Setor de Ciências da Terra da Universidade Federal do Paraná.

Orientador: Dr. Hugo Bornatowski

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em SISTEMAS COSTEIROS E OCEÂNICOS da Universidade Federal do Paraná foram convocados para realizar a arguição da dissertação de Mestrado de **AURORA RUPP** intitulada: **Is a trophic cascade in a subtropical ecosystem real? The ecological role of elasmobranchs in a costal ecosystem of Southern Brazil.**, sob orientação do Prof. Dr. HUGO BORNATOWSKI, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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“Ás incríveis mulheres da minha família, Marion, Rosvita e Bettina que com seu amor, carinho e dedicação, me incentivaram em todos os momentos da vida. E à Luna, que veio mundo em meio ao caos para trazer paz.”

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TEXTO DE DIVULGAÇÃO CIENTÍFICA

E se os tubarões desaparecerem? As populações desses animais estão diminuindo rapidamente em todo o mundo e os cientistas já estão estudando quais as consequências para os oceanos. Como os tubarões são predadores que ocupam o topo da cadeia alimentar, eles ajudam a manter sob o controle o tamanho das populações de todos os organismos que estão abaixo deles na cadeia. Por isso, o declínio das populações dos tubarões pode causar um efeito chamado de efeito de cascata. Sem os predadores de topo, as populações dos mesopredadores, que são aqueles outros peixes carnívoros, raias ou até mesmo tubarões menores, podem aumentar. E, em consequência, o grande número desses mesopredadores acaba gerando a diminuição nas populações de organismos como pequenos peixes e moluscos.

Esse efeito não acontece da mesma forma em todos os locais, por isso as pesquisas são tão importantes. Nós estudamos o papel dos tubarões e das raias no Paraná e, para isso, geramos um modelo ecológico utilizando o software chamado *Ecopath with Ecosim*. Através desse modelo é possível observar as relações entre os organismos do ecossistema e também fazer simulações para ver se o aumento na mortalidade dos tubarões, causado pela pesca, poderia gerar um efeito de cascata.

Através do modelo identificamos que tanto as raias, quanto uma espécie de tubarão menor são mesopredadores, e são influenciados pelos tubarões maiores que são os predadores de topo. Já os tubarões sofrem uma forte pressão da pesca. Através das simulações de pesca, observamos que a diminuição das populações de tubarões pode causar o aumento nas populações de raias, especialmente da raia-chicote (nome científico: *Hypanus guttatus*). Mas apesar desse aumento, não observamos um efeito de cascata para esse local.

A grande diversidade da costa do Paraná pode ser uma vantagem, pois em ambientes diversos é menos provável que um efeito cascata ocorra. Ainda assim, os efeitos de cascata são difíceis de serem comprovados e até mesmo testados, pois dependem de vários fatores, como a diversidade do local, o comportamento dos animais, as alterações que podem ocorrer no ambiente ao longo do tempo, e muitos outros.

RESUMO

Grandes tubarões, geralmente, ocupam os níveis tróficos mais altos e são elos importantes na estruturação das redes tróficas. Porém, o declínio desses predadores vem sendo observado no mundo todo, com taxas de redução populacional alcançando mais de 90% para algumas espécies em algumas regiões. Através desses declínios, acredita-se que o efeito da perda de predadores poderia resultar na liberação de mesopredadores (elos intermediários das redes tróficas) e, consequentemente, a efeitos cascata em toda teia alimentar. Baseado nessa hipótese, o presente estudo objetivou testar se as raias fazem papel de mesopredadores em um ecossistema costeiro do sul do Brasil e se são susceptíveis ao declínio de tubarões. Também testou se o declínio em biomassa dos grandes tubarões conduziria a um efeito de cascata na costa do Paraná. Para isso, um modelo ecotrófico foi criado, baseado em dados confiáveis de biomassa e de alimentação das espécies na região. O software de modelagem de balanço de massas *Ecopath with Ecosim* (EwE) foi usado para avaliar a posição trófica de tubarões e raias, e para compreender quais são suas interações com os demais grupos do ecossistema. Entre os parâmetros do modelo, a costa paranaense mostrou ser um sistema maduro, com uma alta conectividade e média complexidade. Os níveis tróficos da costa variaram de 1 a 4,4, sendo que o nível 4 foi composto por tubarões e as raias pertencendo ao terceiro nível trófico. Os grandes tubarões foram espécies-chave para o ecossistema, influenciando nas populações dos níveis inferiores. Além disso, os tubarões sofreram um forte impacto da pesca. Com base nas simulações de aumento da mortalidade por pesca de tubarões, o aumento de mesopredadores frente ao declínio de grandes tubarões foi evidente na costa do Paraná. No entanto, não foi observado efeitos cascata a partir das simulações realizadas. A alta diversidade do sistema e a redundância entre elasmobrânquios mesopredadores e outros teleósteos podem diminuir as chances de efeito cascata ocorrer.

Palavras-chave: Efeito cascata; Ecopath with Ecosim; Elasmobrânquios; Mesopredadores; Costa do Paraná.

ABSTRACT

Large sharks generally occupy the highest trophic levels and are important links in the structuring of trophic networks. However, the decline of these predators has been observed worldwide, with population reduction rates reaching over 90% for some species. Through these declines, it is believed that the effect of the loss of predators could result in the mesopredators release and, consequently, to cascade effects in the food web. Based on this hypothesis, the present study aimed to test if the batoids and an small shark play the role of mesopredators in a coastal ecosystem in southern Brazil and if are susceptible to large sharks decline. Also, we tested if the decline in biomass of large sharks would lead to a cascade effect on the Paraná coast. For this, an ecotrophic model was performed, based on reliable data on biomass and species feeding in the region. The mass balance modeling software Ecopath with Ecosim (EwE) was used to assess the trophic position of sharks and rays, and to understand what their interactions are with other groups in the ecosystem. Among the parameters of the model, the Paraná coast showed to be a mature system, with high connectivity and medium complexity. The trophic levels of the coast varied from 1 to 4.4, with level >4 composed of sharks, and rays belonging to the third trophic level. Large sharks were keystone species for the ecosystem, influencing populations at lower levels. In addition, sharks were strong impacted by fishing. According to fishing mortality simulations, we observed an increase in mesopredators biomass due of the decline of large sharks. However, no cascade effects were observed from the simulations. The high diversity of the system and the redundancy between mesopredator and other teleosts can decrease the chances of a cascade effect occurring.

Keywords: Cascade effect; Ecopath with Ecosim; Elasmobranchs; Mesopredators; Paraná coast.

SUMÁRIO

IS A TROPHIC CASCADE IN A SUBTROPICAL ECOSYSTEM REAL? THE ECOLOGICAL ROLE OF ELASMOBRANCHS IN A COSTAL ECOSYSTEM OF SOUTHERN BRAZIL.

Cascata trófica em um ecossistema subtropical é real? Função ecológica de elasmobrânquios em um ecossistema costeiro do sul do Brasil**.**

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HIGHLIGHTS

- Large sharks are important links between trophic levels.
- Large sharks are keystone species, and were strong impacted by fishing.
- The decline of larger predators could lead to mesopredator release.
- Despite increase in mesopredator biomass, no cascading events were observed through mortality simulations.

1 INTRODUCTION

Sharks, skates and rays, are widely distributed and comprise approximately 1,139 species (509 species for sharks and 630 for batoids - sensu Weigmann, 2016). Although the number of elasmobranchs is smaller compared to other groups of vertebrates, sharks are evolutionarily very successful organisms, surviving various mass extinctions (Camhi et al. 2007; Stein et al. 2018). Despite this evolutionary success, the extinction risk for Chondrichthyes is substantially higher than for most other vertebrates, predominantly due to overfishing and habitat degradation which combined with biological characteristics such as late sexual maturation and low fertility makes them more vulnerable to environment changes (Simpfendorfer et al. 2011; Dulvy et al. 2014; Stein et al. 2018). Studies suggest that populations of large sharks have declined more than 90% in some regions (e.g. Ferretti et al. 2008; Barausse et al. 2014; Roff et al. 2018). Less understood, however, are the ecological consequences of these declines (Heithaus et al., 2010; Grubbs et al. 2016; Roff et al. 2016a).

Large sharks occupy high positions in marine food webs and therefore act as important regulators of lower trophic level species, playing a fundamental role in marine ecosystems through direct and indirect ecological interactions (e.g. Heithaus et al. 2008; Ferretti et al. 2010; Hussey et al. 2015). Although large sharks are essentially considered to be the apex predators in oceanic, coastal and reef habitats (Myers et al. 2007; Ruppert et al. 2013; Bornatowski et al. 2018), and their declines can lead to cascading effects on lower trophic levels resulting in mesopredator release (Heithaus et al. 2008; Baum & Worm 2009), recent evidence suggests that their trophic cascades or top-down influences may be equivocal (e.g. Grubbs et al. 2016; Roff et al. 2016a; Bornatowski et al. 2018). This uncertainty may negatively influence decisions, such as the incentive of the predatory fishery of rays, which could disturb the conservation and management of these species (see Grubbs et al. 2016 for details).

Empirical data from the northwest Atlantic Ocean suggests that the depletion of large coastal sharks resulted in increased cownose ray (Rhinoptera bonasus) abundance, consequently causing the collapse of commercial bivalve stocks (Myers et al. 2007). However, recent studies suggest that this may not true, due to the lack of temporal data and diet information the trophic cascade as suggested cannot be support (see Grubbs et al. 2016). According to Grubbs et al. (2016), a trophic cascade mediated by predation release should require five steps: 1) correlations between abundance trends of predators and prey, 2) spatiotemporal overlap between predators and prey, 3) rapid grow of prey populations

compared to their predators, 4) precise data on the predator's diet, and 5) predators as the primary reason of predation mortality on the prey.

Based on this discussion and premises, this paper aims to test the hypothesis that rays are intermediary elements of the food web and can respond to the decline of predators and, consequently, influence their prey. Therefore, we first try to understand the ecological role of sharks and rays in a coastal ecosystem of Southern Brazil. We used Ecopath with Ecosim (EwE) mass balance modeling to evaluate the trophic position of species and their actions in the whole ecosystem. This ecosystem is well studied, with abundant feeding, fishing and biomass data. Also, we identify the keystone species in the ecosystem and explored which ones can cause top-down effects. Finally, we performed simulations of changes in fishing effort and shark biomass to understand how these variables affected the ecosystem.

2 METHODS

2.1 Study area and fisheries activities

The Paraná coast, situated in southern Brazil, is approximately 100 km in length. The weather is moderately warm and humid (Vanhoni & Mendonça, 2008), with water temperature ranging from 20 to 28ºC (Brandini et al. 2007). The continental shelf in this area is between 175 and 190 km wide and is predominantly covered by sand, clay, and mud. For the study, we delimited an area that includes the inner shelf to the 20 m isobaths. This area of study comprised ~2800 km^2. The area supports more than 80 species of elasmobranchs (Bornatowski et al. 2009; Spier et al. 2018), and there are strong interactions both among them, and with other organisms (Bornatowski et al. 2014a; Domit et al. 2018).

Fisheries activities on the Paraná coast are exclusively artisanal or small-scale. The boats, which are fiberglass or wooden, operate within up to 25 miles of the coast. The fisheries target different resources during the year, based on seasonal changes in species abundance and tourism. Trawlers target shrimps (Robert et al. 2006; Andriguetto et al. 2009), while gillnets target mainly teleosts and elasmobranchs (Robert and Chaves, 2006; Bornatowski et al. 2011). Monofilament gillnet gear includes both bottom-set and driftnets with mesh sizes ranging from 5 to 40 cm (between opposite knots) (Andriguetto et al. 2009; Bornatowski et al. 2011). Nevertheless, traditional fisheries along the Paraná coast catch large numbers of neonate and juvenile sharks, coastal large sharks, and several species of batoids (Bornatowski et al. 2011). In fisheries monitoring from 2010 to 2012, Guitarfishes

(*Pseudobatos percellens* and *Zapteryx brevirostris*) represented ~50% of total elasmobranch landings off Paraná coast (unpublished data). Hammerhead sharks (*Sphyrna lewini* and *S. zygaena*) represented 17%, and Sharpnose shark (*Rhizoprionodon lalandii*) represented 9%. The Cownose and Stingrays (*Rhinoptera* spp., *Dasyatis* spp. and *Hypanus* spp.) represented 16%. Other sharks such as *Carcharhinus obscurus*, *C. limbatus*, and *Galeocerdo cuvier* represented ~3% of total elasmobranch catches (personal observation).

2.2 Food web modeling using the Ecopath approach

We generated a trophic model using the software Ecopath with Ecosim (Polovina, 1984; Christensen & Walters, 2004; Christensen et al., 2005), using as a base a preview published Ecopath model for Paraná coast (Bumbeer et al., 2017). The model represented the year 2015 as the baseline. In the basic equation of the Ecopath model the consumption by a predator (or group) leads to the mortality of its prey (or group) due to predation. This is mathematically described by a system of linear equations (Christensen & Walters 2004):

$$B_i \text{ x } PB_i \text{ x } EE_i - \sum_j (B_j \text{ x } QB_j \text{ x } DC_{ji}) - EX_i = 0 \qquad \text{(Eq.1)}$$

where Bi is the biomass of group i; PBi is the Production/Biomass rate of i, which is equal to the total mortality Z (Allen, 1971); EEi is the Ecotropic Efficiency of i, which ranges from 0 to 1 and represents the fraction of the production of the group that is used within the system or exported from the system; Bj is the biomass of predator j; QBj is the food consumption per unit of biomass for predator j; DCji is the fraction of i in the diet of j; and EXi is the export of i and represents the biomass that is caught through fishing and/or that migrates to other ecosystems. A detailed introduction of the EwE approach and description of main features, data requirements and limitations can be found in the literature (Christensen & Walters 2004; Link 2010; Steenbeek et al. 2016; Heymans et al. 2016).

The food web model was constructed by selecting functional groups based on interactions between large sharks and batoids, and their relative prey. Some species were grouped, while others remained as single species due to our main goals.

2.3 Functional groups and input data

We used the previous EwE model developed in the region (Bumbeer et al. 2017) to

develop our new model. This new food web model has some original elements, including species of large sharks as individual functional groups: Tiger (*Galeocerdo cuvier*), Dusky (*Carcharhinus obscurus*), Blacktip (*C. limbatus*) and Hammerhead sharks (*Sphyrna lewini* and *S. zygaena*). Also, batoids species were separated as follows: the Cownose ray (*Rhinoptera brasiliensis* and *R. bonasus*), Stingray (*Hypanus guttatus*), Brazilian guitarfish (*Pseudobatos percellens*), and the Shortnose guitarfish (*Zapteryx brevirostris*). Thus, a total of 34 functional groups were used in the present model, with 16 groups of teleosteans, nine groups of elasmobranchs, nine groups of invertebrates, one phytoplankton group, and detritus (Supplementary material A). The functional groups were selected and chosen based on the interactions between species, size, and feeding habits for the region (Bornatowski et al. 2014a,b,c; Bumbeer et al. 2017).

The biomass of demersal teleostean fish in the inner shelf was obtained with experimental trawl-fishing, while data about reef fish came from visual census (see Bumbeer et al. 2017 for more details). When necessary, data from other previous models developed in some marine Brazilian regions were obtained (e.g. Gasalla & Rossi-Wongtschowski, 2004; Araújo & Tubino, 2017; Angelini et al. 2018). When not available, biomass values were estimated from EwE through Ecotrophic Efficiency (EE) collected from the literature regarding similar groups (Supplementary material B).

The production/biomass ratio (PB) was calculated using Pauly's (1980) empirical equation or from the literature (see Supplementary material B). The Consumption/Biomass ratio (QB) was estimated using Palomares and Pauly's (1998) empirical equation or from the literature (Froese and Pauly 2018). We used the Fishbase (Froese and Pauly, 2018) for the input parameters values for equations PB and QB. A diet composition matrix was constructed with data from the literature, using studies from the same study area or similar ecosystems (see Supplementary material C). The diet information for elasmobranchs was obtained from published data of Paraná coast (see Bornatowski et al. 2014b,c).

2.4 *Model analysis and validation*

We used the Pedigree Index of the Ecopath model to quantify the origin and quality of the data, assigning a value to each (B, PB, QB, and diet matrix). The pedigree index varies between 0 (low quality) and 1 (high quality) (Christensen et al., 2008).

The model was considered balanced when estimated EE values were all lower than 1 and were high (~0.95) for exploited species and more predated ones (e.g. sardines), and low

for unexploited top predators (EE<0.5). In addition, values of production/consumption (P/Q) for functional groups were between 0.1 and 0.35 with the exception of some fast growing species, and values of net efficiency were <1 (Christensen et al. 2008). The criteria from the Pre-Balance (PREBAL) approach was also used to analyse the relationship between biomass, PB, and QB values with increasing trophic levels (Link 2010; Heymans et al. 2016).

Several indicators were calculated by Ecopath to provide a general outlook of the ecosystem (sensu Odum, 1969): Total Primary Production/Total Respiration (TPP/TR), Total System Throughput (TST), Total Primary Production/Total Biomass (TPP/TB), Total Biomass/Total System Throughput (TB/TST), Connectance Index (CI), System Omnivory Index (SOI) and Overhead (O). We are also able to analyze the feeding strategy for each functional group by using the Omnivory Index (OI, Christensen et al. 2008). These attributes measure the development status for the ecosystem (sensu Odum, 1969), under the assumption that "mature" environments are more resilient than "immature" ecosystems (see Angelini et al., 2013).

A Mixed Trophic Impact (MTI) analysis was used to quantify the relative impact of a component (impacting group) on each of the other components (impacted groups) in the food web, including fishing fleet (Ulanowicz and Puccia 1990, based on Leontief 1951). The MTI provides two estimated parameters: the trophic impact component (Ɛi) and the relative biomass component (pi), which are used to estimate keystone species indices. Parameter Ɛi represents the overall direct or indirect trophic effect of group i on all the other groups in the food web:

$$\varepsilon_i = \sqrt{\sum_{j \neq i} m_{ij}^2} \qquad \text{(Eq. 2)}$$

where Ɛi is expressed as the sum of the squared values of mij of group i, paired with each of the other living group j and mij is the effect of group i on j, which could be positive (if the impacted group's biomass increases) or negative (if it decreases). The m of group i on itself (mii) is excluded, as well as the m on non-living groups such as detritus (Libralato et al. 2006).

Parameter pi corresponds to the contribution of group i to the total biomass in the food web:

$$p_i = \frac{B_i}{\sum_{k=1}^{n} B_k} \qquad \text{(Eq. 3)}$$

where Bi is the biomass of group i, and Bk the biomass of each one of the n living groups in the food web (Power et al. 1996, Libralato et al. 2006).

To identify the key species within the ecosystem (both keystone and structuring species), we calculated the keystoneness index (KS) using three methods (Libralato et al., 2006, Power et al., 1996). A keystone group plays an important role in the ecosystem regardless of its relatively low biomass (Power et al., 1996). On the contrary, a dominant or structuring group would play an important role due to its large biomass. Both methods use the relative overall effect (εi) calculated from the MTI analysis.

We calculated the keystoneness index (KS) to identify the key species. A keystone species is defined as a species with low relative biomass but which plays an important role in the food web (Paine 1995; Power et al., 1996). Besides, a key species can be a dominant group that play an important role due to its large biomass (Libralato et al. 2006). The model estimated three keystone species indices (KS): KS1 (Libralato et al. 2006), KS2 (adapted from Power et al. 1996), and KS3 (Valls et al. 2015). The indices were obtained by combining Ɛi and pi for each group i, such as:

$$KS_{1i} = \log\left[\varepsilon_i \text{ x } (1 - p_{i)}\right] \quad \text{(Eq. 4)}$$

$$KS_{2i} = \log\left[\varepsilon_i \text{ x } (1/p_{i)}\right] \quad \text{(Eq. 5)}$$

The KS3 index (Valls et al. 2015) was obtained from:

$$KS_3 = IC_L \text{ x } BC_0 \quad \text{(Eq. 6),}$$

where: ICL (Impact Component) is estimated from Eq. 1 (εi) and BC0 (the Biomass Component) is estimated from Eq. 2 (pi), where BC_0 is the biomass in a descending order ranking (see Valls et al. 2015 for more details).

2.5 *Time-dynamic simulations with Ecosim*

The temporal-dynamic model of EwE, the Ecosim model (Walters et al. 1997; Christensen and Walters 2004), uses the baseline Ecopath model as the initial conditions. The system of linear equations based on Eq. 1 is transformed into a system of ordinary differential

equation as follows (Walters et al. 1997, 2000) (Equation 7):

$$dB_i / dt = g_i x \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) x B_i \quad \text{(Eq. 7)}$$

where dBi/dt is the change in B of group i over time t, gi is the net growth efficiency, Qji is the consumption of group j by group i, Qji is the consumption of group i by group j, M is the number of predator groups, Ii is immigration of group i, MOi is the non-predation rate of natural mortality of group i, Fi is the fishing mortality of group i, and ei is the emigration of group i.

The quantification of prey i consumed by predator j (Qji) is a nonlinear relationship based on the "foraging arena concept" acting on the consumption rates of predators and prey (Walters et al. 2000; Walters and Christensen 2007; Ahrens et al. 2012) (Equation 8):

$$Q_{ij} = \frac{a_{ij} x v_{ij} x B_i x B_j}{2 x v_{ij} x a_{ij} x B_j} \quad \text{(Eq. 8)}$$

Where a_{ij} is the effective search rate of predator $_j$ feeding on prey $_i$, B_i is the biomass of the prey, B_j is the predator biomass, and v_{ij} is the vulnerability of prey $_i$ to predator $_j$. The foraging arena concept implies that the prey biomass is divided into vulnerable and non-vulnerable components and the transfer rate between these two components is the vulnerability rate (v_{ij}). This rate determines whether the flow control is top-down ($v_{ij} > 2$) where increase in predator biomass are directly proportional to increases in predation mortality, bottom-up ($v_{ij} < 2$) where increase in predator biomass will not cause substantial increase in predation mortality on its prey, or mixed ($v_{ij} = 2$; the defaults values in EwE).

After model calibration, we used the Ecosim tool to evaluate changes in a hypothetical 50-year time series. We ran six simulations: i) Increasing fishing effort (FE) by twofold and maintaining the vulnerability rate (v_{ij}) as 2 for all groups ($v_{ij} = 2$ is the default values in EwE). ii) Increasing FE by twofold and changing the v_{ij} for sharks to 10. iii) decreasing FE by 50% and maintaining $v_{ij} = 2$ for all groups. iv) decreasing FE by 50% and changing the v_{ij} for sharks to 10. v) increasing shark mortality by twofold and maintaining $v_{ij} = 2$ for all groups. vi) increasing sharks mortality by twofold and changing the v_{ij} for sharks to 10. A vulnerability rate >2 indicates species capacity to increase mortality through predation, exerting a top-down control in the environment.

3 RESULTS

The Pedigree index value for the southern Brazil model showed high data quality (0.60). The model was considered balanced in relation to the criteria applied to production/consumption, respiration/assimilation, respiration/biomass and net efficiency. Also, the model respected the PREBAL criteria (see Supplementary material D).

Ecopath estimated the biomass values for ten compartments (Table 1), and just a few input values were modified to balance the model (Supplementary material C). The balanced model outputs are presented in Table 1, and the Diet Matrix Composition in Supplementary material C.

Trophic Levels in the model ranged from 1 (e.g. Phytoplankton) to 4.4 (e.g. Dusky Shark). Sharks represent tertiary consumers and, therefore, were the top predators in the food web. Rays represented the second trophic level and were considered mesopredators. Dusky sharks occupying the highest trophic level, their omnivory index is low (0.17). However, Tiger sharks and Squids were considered as the most generalist (OI=0.85 and 0.84 respectively) (Table 1).

The Paraná coast model showed a mature ecosystem with a high connectance index (CI = 0.2) and moderate complexity (SOI = 0.2). The Total System Throughput was 11417.4 t/km2, Total Primary Production/Total Respiration was 1.5, Total Biomass /Total System Throughput per year was 0.009, and Overhead was high 77.4% (Table 2).

Table 1 - Basic input parameters and outputs for Paraná coast Ecopath model. The bold values were estimated by Ecopath. TL: Trophic level; B: Biomass (t/km2); P/B: Production/Biomass (year-1); Q/B: Consumption/Biomass (year-1); EE: Ecotrophic Efficiency; OI: Omnivory Index.; Catch (t/km2/year).

Group	Group name	TL	B	P/B	Q/B	EE	OI	Catch
1	Phytoplankton	**1.0**	24.17	152.80	0	**0.33**	**0**	
2	Zooplankton	**2.0**	7.60	40.00	160.00	**0.91**	**0**	
3	Polychaeta	**2.2**	**3.30**	70.00	354.00	0.90	**0.24**	
4	Bivalves and Gastropoda	**2.4**	**3.19**	37.72	233.50	0.85	**0.34**	0.18
5	Other benthos	**2.3**	**33.23**	5.36	16.09	0.95	**0.28**	0.04
6	Shrimps	**2.0**	8.70	6.50	18.00	**0.52**	**0**	0.30
7	Squids	**3.4**	0.40	4.35	11.35	**0.33**	**0.84**	0.010
8	Lutjanidae	**3.6**	0.15	0.30	3.50	**0.02**	**0.53**	0.000633
9	Swimming crabs	**3.0**	**5.67**	2.00	8.00	0.76	**0.33**	0.140
10	Mackerel	**3.6**	0.10	0.26	4.20	**0.69**	**0.58**	0.017232
11	Reef herbivorous	**2.0**	1.27	1.16	27.45	**0.04**	**0**	
12	Reef planctivorous	**3.2**	0.44	1.19	10.90	**0.05**	**0.13**	0.007
13	Reef carnivorous	**3.0**	0.28	0.78	6.60	**0.07**	**0.18**	0.00745
14	Triggerfish	**3.2**	0.73	0.44	5.60	**0.01**	**0.14**	0.003697
15	Blue Runner	**3.4**	0.20	0.78	6.00	**0.18**	**0.18**	0.002
16	Planctivorous	**2.4**	4.55	1.44	25.63	**0.99**	**0.25**	0.190

17	Small carnivorous	**3.3**	1.87	1.71	10.17	**0.66**	**0.05**	0.004252
18	Zoobentivorous	**3.2**	3.18	1.21	8.90	**0.24**	**0.14**	0.096886
19	Intermediate carnivorous	**3.4**	2.44	1.44	8.63	**0.23**	**0.20**	0.100
20	Large carnivorous	**3.5**	2.40	0.63	5.77	**0.43**	**0.38**	0.330
21	Croacker	**3.3**	0.34	0.94	4.30	**0.35**	**0.01**	0.100
22	Cutlassfish	**3.8**	0.20	0.54	3.39	**0.98**	**0.53**	0.001
23	Catfish	**3.2**	1.70	1.19	11.71	**0.03**	**0.17**	0.0675
24	Weakfish	**3.6**	0.50	0.61	6.20	**0.87**	**0.62**	0.09976
25	Cownose rays	**3.4**	**0.12**	0.27	4.10	0.20	**0.04**	0.00126449
26	Shortnose guitarfish	**3.3**	0.17	0.56	7.00	**0.04**	**0.08**	0.00410909
27	Guitarfish	**3.7**	0.10	0.31	4.80	**0.11**	**0.31**	0.00347209
28	Stingray	**3.2**	0.01	0.50	6.35	**0.99**	**0.07**	0.00025936
29	Blacktip shark	**4.1**	**0.002**	0.39	2.80	0.30	**0.24**	0.0002
30	Dusky Shark	**4.4**	**0.009**	0.09	1.80	0.40	**0.17**	0.00035722
31	Tiger shark	**4.3**	**0.003**	0.25	2.00	0.20	**0.85**	0.00016417
32	Hammerhead sharks	**4.3**	**0.04**	0.14	2.05	0.50	**0.20**	0.00269487
33	Brazilian sharpnose shark	**4.3**	**0.02**	0.55	5.40	0.50	**0.11**	0.003
34	Detritus	**1.0**				**0.57**	**0.34**	

Table 2 - Ecosystems attribute revealed by the Paraná coast Ecopath model.

Parameter	Value	Units
Sum of all consumption	4142.8	t/km^2/year
Sum of all exports	1464.1	t/km^2/year
Sum of all respiratory flows	2387.0	t/km^2/year
Sum of all flows into detritus	3423.4	t/km^2/year
Total system throughput	11417.4	t/km^2/year
Sum of all production	4620.4	t/km^2/year
Mean trophic level of the catch	2.8	
Gross efficiency (catch/net p.p.)	0.00046	
Calculated total net primary production	3693.1	t/km^2/year
Total primary production/total respiration	1.5	
Net system production	1306.1	t/km^2/year
Total primary production/total biomass	34.4	
Total biomass/total throughput	0.009	/year
Total biomass (excluding detritus)	107.0	t/km^2
Total catch	1.7	t/km^2/year
Connectance Index	0.22	
System Omnivory Index	0.23	
Ecopath pedigree index	0.60	
Overhead	77.4	%

The groups had different effects on other components according to Mixed Trophic Impact analysis. Hammerhead sharks showed a high negative impact on Stingrays and Cownose rays. Dusky sharks showed a high negative impact on Lutjanidae, followed by minor impacts on Cownose rays and Brazilian sharpnose sharks (Figure 1). Tiger sharks showed a moderate negative impact on Blacktip sharks. Brazilian sharpnose sharks showed a moderate negative impact on reef carnivores, and a moderate positive impact on reef herbivores (Figure 1).

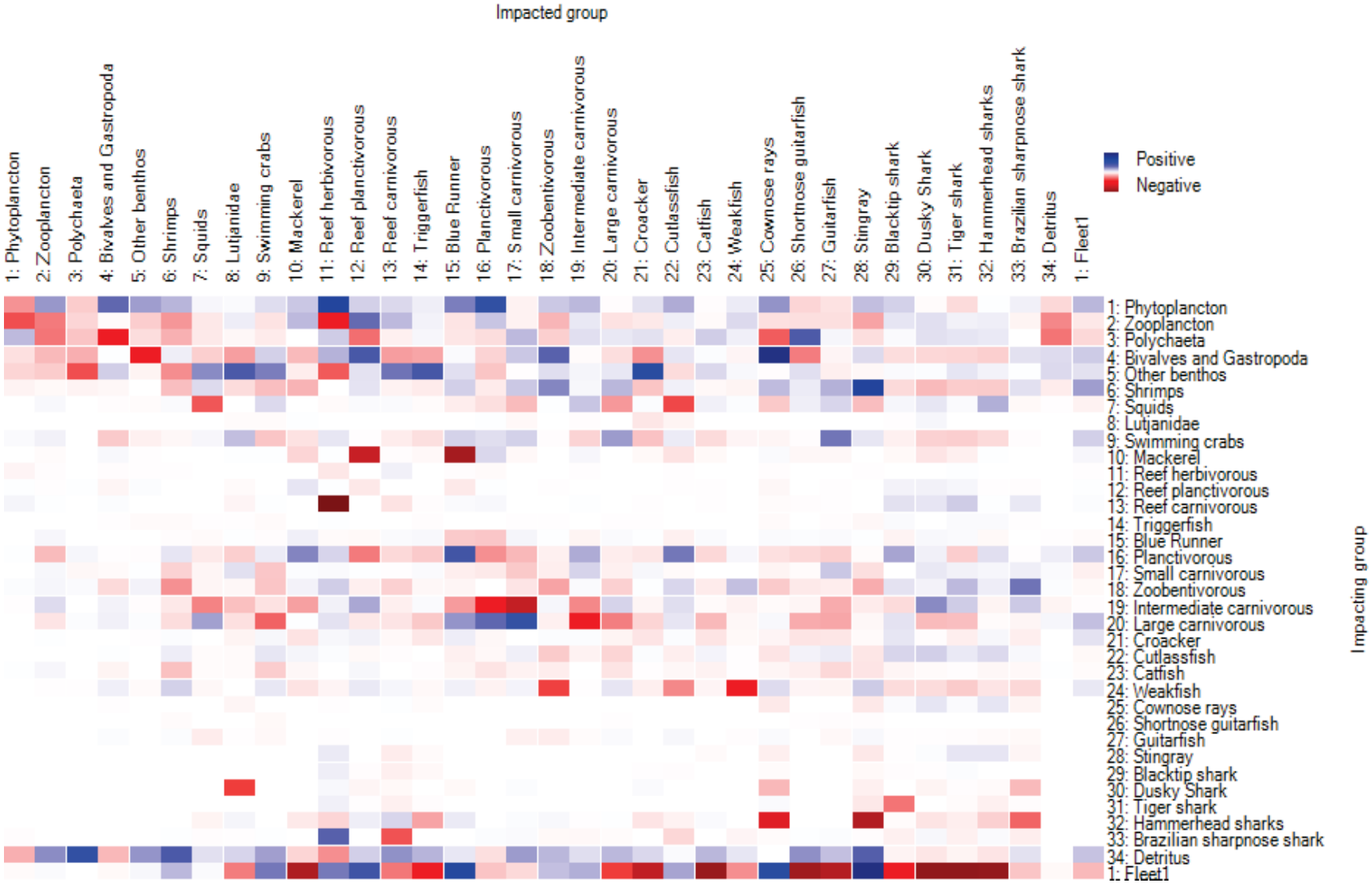

Figure 1- Mixed trophic impact matrix of the Paraná coast Ecopath model. Rows: impacting group; Columns: impacted group. Blue: positive impact; Red: negative impact.

The groups of rays did not show any major impacts on the other groups. However, the invertebrates showed different impacts (both negative and positive) on the rays (Figure 1).

Among sharks, Hammerhead sharks had the highest influence on other components, thus defining them as a keystone species by the three indexes used (Table 3), and the principal keystone species by KS3 (Valls et al. 2015). All of the top five keystone species were sharks by KS2 (sensu Power et al. 1996). The KS1 index (sensu Libralato et al. 2006), considers species based on large biomass and strong trophic interactions. Bivalves and Gastropoda are the principal keystone species by this index, followed by Mackerel and Hammerhead sharks. No ray group was in the top five keystone species in the three indices used (full list – Supplementary material E).

Table 4 Top five Keystone species by each index. Sharks are in bold.

KS1 (Libralato et al. 2006)	KS2 (Power et al. 1996)	KS3 (Valls et al. 2015)
Bivalves and Gastropoda	**Tiger shark**	**Hammerhead sharks**
Mackerel	**Dusky Shark**	Mackerel
Hammerhead sharks	**Hammerhead sharks**	Reef carnivorous
Intermediate carnivorous	**Brazilian sharpnose shark**	**Brazilian sharpnose shark**
Reef carnivorous	**Blacktip shark**	**Dusky Shark**

3.1 Simulation fishing results

The first simulation increasing FE by twofold and maintaining the vulnerability = 2 showed a reduction in the relative biomass of Blacktip (35.0%), Dusky (64.4%), Hammerhead (84.2%) and Brazilian sharpnose sharks (19.2%), and an increase of 44.7% for Tiger sharks. Stingrays had the largest increase, reaching 353.1% of their original value. Shortnose guitarfish, Guitarfish and Cownose rays showed an increase of 2.3%, 3.7% and 7.5% respectively (Figure 3). Among teleostean fish and invertebrates, two groups were most affected by the FE simulation, with a reduction in the relative biomass of Mackerel (99.8%) and Croacker (70.7%). Cutlassfish and Blue Runner increased by 10%. The remaining groups showed minimal or no changes (Figure 2).

In the second scenario, maintaining the twofold FE and changing the vulnerability=10 for top predator sharks (e.g. Blacktip, Dusky, Hammerhead and Tiger sharks), declines were observed (Figure 2). Blacktip, Dusky and Hammerhead sharks declined between 80% and 99%. Tiger and Brazilian sharpnose sharks showed a reduction in their biomasses of 2.2% and 11.3% respectively. Stingrays increased by 680% in relative biomass, and Cownose rays

increased by 9.4%. Shortnose guitarfish and Guitarfish did not differ from the first simulation. Changing the vulnerability rate also favored Cutlassfish, but generated minimal changes among other groups (Figure 2).

For the third scenario decreasing FE by 50% and maintaining vulnerability = 2 for all groups, we observed an increase in the relative biomass of Brazilian sharpnose (9%), Tiger (9.7%), Blacktip (15.8%), Dusky (29.5%) and Hammerhead sharks (38.1%). In contrast to prior simulations, Stingrays (36.1%) and Cownose rays (2.7%) decreased. We also observed an increase in Mackerel (42.1%), Croacker (10.4%) and Weakfish (10.2%), and a decline in relative biomass in 9.2% for Cutlassfish (Figure 2).

The fourth scenario, changing top predator sharks vulnerability = 10, and decreasing FE by 50%, we observed an increase in relative biomass of Tiger (58.3%), Blacktip (68.4%), Dusky (102.0%) and Hammerhead sharks (183.0%). Meanwhile, Brazilian sharpnose shark showed an increase of 21.9% in the first 6 years of simulation, followed by a decline of 31% of original biomass by the end of 50 years. Stingrays were extinct in 48 years and Cownose rays declined by 28.2%. Modifying the vulnerability rate did not change the results for Shortnose guitarfish and Guitarfish (Figure 2).

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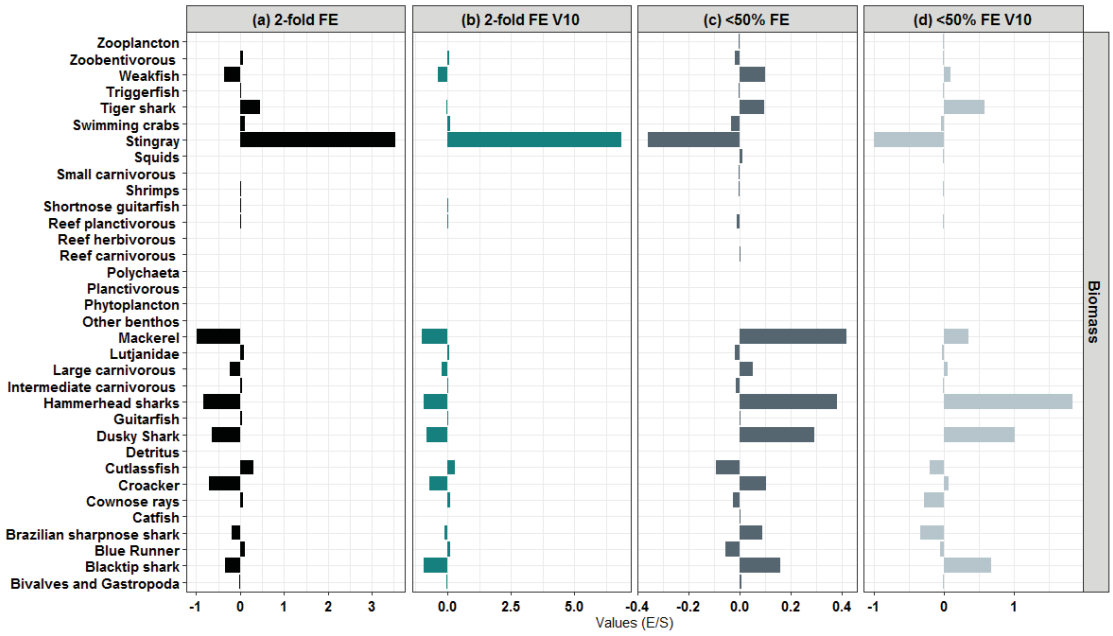

Figure 2 Group relative biomass (end/start) after a 50-year simulation under the following scenarios:. a) Increasing FE by twofold and maintaining v_{ij} = 2 for all groups. b) Increasing FE by twofold and changing sharks v_{ij} for 10. c) Decreasing FE by 50% and maintaining v_{ij} =2. d) Decreasing FE by 50% and changing v_{ij} for 10.

In the fifth scenario, shark mortality was increased by twofold and vulnerability was

kept at 2 for all groups. We observed a reduction in relative biomass of Blacktip (25.1%), Dusky (59.6%) and Hammerhead sharks (80.1%). An increase was observed for Tiger shark (50.6%), and Brazilian sharpnose shark (25.8%). Stingrays and Cownose rays showed a strong increase of 365% and 13.5% respectively.

However, in the sixth simulation with apex shark vulnerability set to 10, the relative biomass of Blacktip shark, Dusky shark and Hammerhead sharks declined between 77.5% and 90.4%. However, an increase was observed for Brazilian Sharpnose sharks (29.7), Tiger sharks (26.5%), Stingrays (747.1%), and Cownose rays (15.4%) (Figure 3).

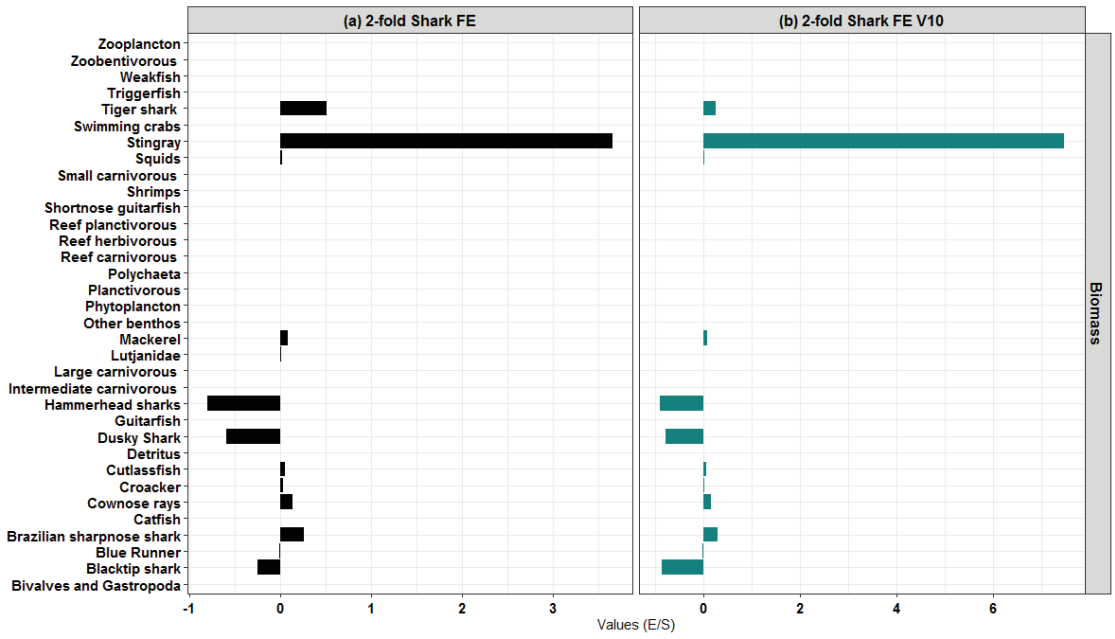

Figure 3 Group relative biomass (end/start) after a 50-year simulation under the following scenarios. a) increase in shark mortality by twofold and maintaining $v_{ij} = 2$ for all groups. b) increase in shark mortality by twofold and changing shark v_{ij} to 10.

4 DISCUSSION

Understanding the effects of top predator removal on marine ecosystems is complex (Hussey et al. 2014, 2015). Sharks are often classified as keystone species in coastal ecosystems (Navia et al. 2010; Bevilacqua et al 2016; Bornatowski et al. 2014a; Fourriére, et al 2019), reef environments (Roff et al 2016b) and pelagic habitats (e.g. Griffiths et al. 2010; Bornatowski et al. 2018). However, while studies have shown that removal of large sharks (>3 m total length - TL) and large marine teleosteans (e.g. billfish and tunas) has a profound impacts on the food chain (e.g. Stevens et al. 2000; Kitchell et al. 2006; Myers et al. 2007;

Ferretti et al. 2010; Britten et al. 2014), others have indicated that effects, after shark species loss, were not so persistent on trophic relationships (e.g. Kitchell et al. 2002; Griffiths et al. 2010). In our study, all sharks were classified as keystone species. Although large sharks did show negative influences on the intermediate levels, simulations involving a reduction of large shark biomass did not have consistent effects within the food web. An increase in mesopredator biomass after large shark biomass reduction was observed, but strong trophic cascades were not.

Conventionally, small elasmobranchs (< 1.5 m TL) are prey of large marine animals, and are classified as mesopredators. The Brazilian sharpnose shark, *Rhizoprionodon lalandii*, is a small shark (~75 cm TL), very common in coastal habitats from southeastern to southern Brazil (Motta et al. 2005). Their small size is a determinate of their ecological role (Navia et al. 2017), and this species comprises part of the diet of large sharks such as hammerhead, dusky and tiger sharks (Bornatowski et al. 2014b). In our model, this species showed a high trophic level (TL = 4.3), being classified as mesopredator shark. However, this species could operate in a 'top-predator' function in the absence of large sharks (see Bornatowski et al. 2014a). Based on our simulations, however, after a reduction in large shark biomass we did not observe changes in Brazilian sharpnose shark biomass. An increase in fishing effort resulted in the population decline of top predators, and also a decline of Brazilian sharpnose shark biomass. This result differs from that found by Bornatowski et al. (2014a), in which the Brazilian sharpnose shark would benefit from the decline of its predators. However, in scenarios decreasing the fishing effort, Brazilian sharpnose shark biomass increased rapidly. This corroborates their faster recovery potential due to early sexual maturation in small sharks (Lessa et al., 2009; Bornatowski et al., 2012). However, when we changed the vulnerability rate (v=10; top-down control), the biomass of hammerhead sharks and dusky sharks increased, and Brazilian sharpnose shark biomass decreased after 6 years. This indicates that these animals would only benefit from reduced fishing if their predators do not exert a strong top-down effect.

The batoid group (rays, skates, and guitarfishes) also are commonly considered as mesopredators in many ecosystems (e.g. Myers et al. 2007; Vaudo et al. 2010; Navia et al. 2011; Bornatowski et al. 2014a). The species Stingray (*Hypanus guttatus*), Shortnose guitarfish (*Zapteryx brevirostris*), Cownose ray (*Rhinoptera* spp.) and Guitarfish (*Pseudobatos percellens*) occupied the third trophic position in the Paraná coast ecosystem (Bornatowski et al. 2014a; Bumbeer et al 2017). Stingray appeared as the seventh keystone species in KS2 index, and in the seventeenth position on KS3 index. This species was the best

positioned batoid in the indexes. Shortnose guitarfish was considered as keystone species by topological analysis in Bornatowski et al. (2014a), however in the present model this species appeared below of 20th position. In the topological analysis the abundance and fishing pressure are not considered (Navia et al. 2010). Based on simulations, the batoid group was strongly impacted by lower levels such as Squids, Polychaeta, Bivalves/Gastropoda and Shrimps and by higher levels such as Hammerhead and Dusky sharks. But the batoids themselves do not exert strong impacts on either lower nor higher levels. This had been observed by other studies in southern Brazil (Angelini et al 2018; Bornatowski et al. 2017; Bumbeer et al. 2017), in the Pacific (Fourriére et al. 2019), and in Mediterranean waters (Coll et al. 2013). In contrast, in Bay of Bengal, rays had strong impacts on lower trophic levels (Karim et al 2019). The functional redundancy between batoids and other mesopredators (teleosts and squids) could be an explanation for the low impact of rays in the mixed trophic impact analyses and for the non-occurrence of a cascade effect in this ecosystem (Frisch et al., 2016).

Hammerhead sharks, Sphyrna spp., are predators of batoids, mainly stingrays (Strong et al, 1990, Hoffmayer et al 2013, Bornatowski et al 2014c) this predation effect was also evident in our simulations. The stingray, *H. guttatus*, was the only batoid species that responded significantly to shark biomass changes. In the four scenarios where hammerhead shark biomass declined, Stingray increased between 300% and 700%. Cownose rays increased to only a small extent, in contrast to the hypothesis of Myers et al. (2007), in which cownose rays had a significant increase. Also, the increase of a single mesopredator is not enough to cause a trophic cascade. In addition, according to indirect effects some species can benefit from the reduction of others. For instance, tiger sharks increased in biomass when other large sharks declined. This probably was related to competition release, as has been observed in other ecosystems (Bornatowski et al. 2018).

Trophic cascade events are not easy to identify (Grubbs et al. 2016). For a trophic cascade to occur it is important that mesopredadors have a low rate of fishing mortality. Predation and competition are more evident when they are not confounded with high rates of fishing mortality (Ferretti et al, 2010; Ferretti et al 2013). In the Paraná coast ecosystem, both sharks and batoids had high fishing mortality rates. Therefore, the influences of large predators and mesopredators are influenced by fishing (Ferretti et al, 2010, 2013; Grubbs et al. 2016; Roff et al. 2016a).

Even robust models have limitations, making it difficult to prove complicated effects such as trophic cascades (Navia et al, 2010; Ruppert et al, 2013). However, EwE models

provide a useful framework for evaluating trophic cascades, mainly when precise diet information, biomass, production, and consumption rates are accurately defined for every group (Roff et al. 2016a).

A factor not considered by EwE models is that cascades can be induced by risk effect (Burkholder et al. 2013; Bond et al 2019, Rasher et al 2017), in which only the presence of the top predator is sufficient to modify the behavior of the mesopredators. This consequently changes the intensity of mesopredator predation on lower trophic level species (Heithaus et al., 2008; Ferretti et al., 2010; Burkholder et al. 2013). In addition, the simulations often did not account for anthropogenic changes, climate change and/or other phenomena that can influence the availability of resources and even the distribution of species. Therefore, we suggest that future studies should consider other factors and variables to better explain the effects in the ecosystem.

We need to take care to avoid losing keystone species. Indeed, large sharks did not have high influence on the biomass of the lower levels of the food chain. However, the loss of these species may have greater effects on the community in the future, mainly because some food networks have become less diverse, less robust and more unstable, and this may be directly linked to overexploitation by human populations (Yeakel & Dunne, 2015).

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SUPPLEMENTARY MATERIAL A – FUNCTIONAL GROUPS DESCRIPTION

n.	Group name	Species
1	Phytoplankton	
2	Zooplankton	
3	Polychaeta	
4	Bivalves and Gastropoda	
5	Other benthos	
6	Shrimps	*Farfantepenaeus paulensis, Litopenaeus schmitti, Xiphopenaeus kroyeri*
7	Squids	*Lolliguncula brevis, Doryteuthis plei*
8	Lutjanidae	*Lutjanus analis, L. cyanopterus, L. jocu*
9	Swimming crabs	*Callinectes spp., Arenaeus cribrarius*
10	Mackerel	*Scomberomorus brasiliensis*
11	Reef herbivorous	*Acanthurus chirurgus, Sparisoma frondosum*
12	Reef planctivorous	*Chloroscombrus chrysurus, Chromis multilineata*
13	Reef carnivorous	*Anisotremus virginicus, Chaetodipterus faber, Haemulon aurolineatum, Haemulon steindachneri, Orthopristis ruber, Pareques acuminatus*
14	Triggerfish	*Balistes capriscus*
15	Blue Runner	*Caranx crysos*
16	Planctivorous	*Anchoa januaria, Cetengraulis edentulus, Sardinella brasiliensis*
17	Small carnivorous	*Sphoeroides greeleyi, Ctenosciaena gracilicirrhus, Etropus crossotus*
18	Zoobentivorous	*Eucinostomu argenteus, Larimus breviceps, Paralonchurus brasiliensis, Pomadasys corvinaeformis, Sphoeroides testudineus*
19	Intermediate carnivorous	*Stellifer brasiliensis, S. rastrifer, Diapterus rhombeus, Oligoplites saliens, Citharichthys spilopterus, Isopisthus parvipinnis*
20	Large carnivorous	*Centropomus parallelus, Cynoscion jamaicensis, Menticirrhus americanus, M. littoralis*
21	Croacker	*Micropogonias furnieri*
22	Cutlassfish	*Trichiurus lepturus*
23	Catfish	*Cathorops spixii, Genidens genidens*
24	Weakfish	*Macrodon ancylodon*
25	Cownose rays	*Rhinoptera bonasus, R. brasiliensis*
26	Shortnose guitarfish	*Zapteryx brevirostris*
27	Guitarfish	*Pseudobatos percellens*
28	Stingray	*Hypanus guttata*
29	Blacktip shark	*Carcharhinus limbatus*
30	Dusky Shark	*Carcharhinus obscurus*
31	Tiger shark	*Galeocerdo cuvier*
32	Hammerhead sharks	*Sphyrna lewini and S. zygaena*
33	Brazilian sharpnose shark	*Rhizoprionodon lalandii*
34	Detritus	

SUPPLEMENTARY MATERIAL B – ORIGINAL VALUES AND REFERENCES OF DATA USED TO BUILD THE PARANÁ COAST MODEL

Original Input Values							
n.	**Groups**	**B**	**PB**	**QB**	**Landings**	**Discard**	**EE**
1	Phytoplancton	24.17	152.80				
2	Zooplancton	7.30	40.00	160.00			
3	Polychaeta		70.00	354.00			
4	Bivalves and Gastropoda		37.72	233.50			
5	Benthos		5.36	16.09			
6	Shrimps	8.70	6.50	18.00	0.3		
7	Squids	3.75	4.35	11.35	0.01		
8	Lutjanidae	0.15	0.31	3.50	0.000633		
9	Swimming crabs		2.00	8.00			
10	Mackerel	0.10	0.26	4.20	0.017232		
11	Reef herbivorous	1.27	1.16	27.45			
12	Reef planctivorous	0.23	1.07	10.50	0.073478	0.001113	
13	Reef carnivorous	0.28	0.78	6.60	0.00745	4.00E-05	
14	Triggerfish	0.73	0.44	5.60	0.003697		
15	Blue Runner	0.20	0.78	6.00	0.018954		
16	Planctivorous	4.30	1.45	25.63	0.202033	0.00203	
17	Small carnivorous	1.87	1.71	10.17	0.004252	0.003311	
18	Zoobentivorous	3.15	1.21	8.90	0.096886	0.898503	
19	Intermediate carnivorous	1.70	1.44	8.63	0.10584	0.156204	
20	Large carnivorous	2.44	0.63	5.78	0.33555	0.007305	
21	Croacker	0.34	0.94	4.30	0.101825	0.002225	
22	Cutlassfish	0.20	0.54	3.39	0.001	0.0003	
23	Catfish	1.70	1.19	11.71	0.0675	0.03337	
24	Weakfish	0.50	0.61	6.20	0.09976	0.00075	
25	Cownose rays		0.27	4.10	0.00126449		

n.	Groups	B	PB	QB	Landings	Discard	EE
26	Shortnose guitarfish	0.17	0.56	7.00	0.00410909		
27	Guitarfish	0.10	0.31	4.80	0.00347209		
28	Stingray	0.01	0.50	6.35	0.00025936		
29	Blacktip shark		0.39	2.80	7.17E-05		0.05
30	Dusky Shark		0.09	1.80	0.00035722		0.05
31	Tiger shark		0.25	2.00	0.00016417		0.03
32	Hammerhead sharks		0.14	2.05	0.00269487		0.7
33	Brazilian sharpnose shark		0.55	5.40	0.0015		0.7
34	Detritus						

		Refereces		
n.	Groups	Biomass	Production/Biomass	Consumption/Biomass
1	Phytoplancton	Bumbeer et al. (2017)	Rocha et al (2007)	
2	Zooplancton	Bumbeer et al. (2017)	Rocha et al (2007)	Rocha et al (2007) and Angelini et al. (2018)
3	Polychaeta	Estimated from Ecopath	Rocha et al (2007)	Angelini et al. (2018)
4	Bivalves and Gastropoda	Estimated from Ecopath	Rocha et al (2007)	Angelini et al. (2018)
5	Other benthos	Bumbeer et al. (2017)	Rocha et al (2007)	Angelini et al. (2018)
6	Shrimps	Bumbeer et al. (2017)	Gasalla & Rossi-Wongtschowski (2004)	Gasalla & Rossi-Wongtschowski 2005
7	Squids	Estimated from Ecopath	Gasalla & Rossi-Wongtschowski (2004)	Gasalla & Rossi-Wongtschowski 2005
8	Lutjanidae	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
9	Swimming Crabs	Estimated from Ecopath	Lira et al. (2018)	Lira et al. (2018)
10	Mackerel	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
11	Reef herbivorous	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
12	Reef planctivorous	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
13	Reef carnivorous	Bumbeer et al. (2017) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
14	Triggerfish	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
15	Blue Runner	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)

n.	Groups	Biomass	Production/Biomass	Consumption/Biomass
16	Planctivorous	Bumbeer et al. (2017) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
17	Small carnivorous	Bumbeer et al. (2017) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
18	Zoobentivorous	Bumbeer et al. (2017) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
19	Intermediate carnivorous	Bumbeer et al. (2017) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
20	Large carnivorous	Bumbeer et al. (2017) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
21	Croacker	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
22	Cutlassfish	Angelini et al. (2018)	Angelini et al. (2018)	Angelini et al. (2018)
23	Catfish	Angelini et al. (2018) and personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
24	Weakfish	Bumbeer et al. (2017)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
25	Cownose rays	Estimated from Ecopath	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
26	Shortnose guitarfish	personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
27	Guitarfish	personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
28	Stingray	personnal data (trawl nets)	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
29	Blacktip shark	Estimated from Ecopath	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
30	Dusky Shark	Estimated from Ecopath	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
31	Tiger shark	Estimated from Ecopath	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
32	Hammerhead sharks	Estimated from Ecopath	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
33	Brazilian sharpnose shark	Estimated from Ecopath	Pauly (1980) equation	Empirical regression of Palomares and Pauly (1998)
34	Detritus			

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SUPPLEMENTARY MATERIAL C – DIET MATRIX COMPOSITION AND REFERENCES

	Prey/predator	2	3	4	5	6	7	8	9	10	11
1	Phytoplancton	0.45	0.1	0.3	0.35	0.3	0	0	0	0.01	0.85
2	Zooplancton	0	0.08	0.1	0.1	0	0.01	0.09	0	0.07	0
3	Polychaeta	0	0.02	0.1	0.15	0	0	0	0.21	0	0
4	Bivalves and Gastropoda	0	0.05	0	0.02	0	0	0	0.25	0	0
5	Other benthos	0	0.05	0.1	0	0	0.3	0.35	0.3	0.06	0
6	Shrimps	0	0	0	0.01	0	0.1	0.02	0.005	0.03	0
7	Squids	0	0	0	0	0	0.05	0	0	0.02	0
8	Lutjanidae	0	0	0	0	0	0	0	0	0	0
9	Swimming crabs	0	0	0	0	0	0.001	0.16	0	0	0
10	Mackerel	0	0	0	0	0	0	0	0	0	0
11	Reef herbivorous	0	0	0	0	0	0	0	0	0	0
12	Reef planctivorous	0	0	0	0	0	0	0	0	0.05	0
13	Reef carnivorous	0	0	0	0	0	0	0	0	0	0
14	Triggerfish	0	0	0	0	0	0	0	0	0	0
15	Blue Runner	0	0	0	0	0	0	0	0	0.06	0
16	Planctivorous	0	0	0	0	0	0.02	0	0	0.37	0
17	Small carnivorous	0	0	0	0	0	0.02	0.07	0	0	0
18	Zoobentivorous	0	0	0	0	0	0.009	0	0	0.02	0
19	Intermediate carnivorous	0	0	0	0	0	0.01	0.01	0	0	0
20	Large carnivorous	0	0	0	0	0	0.05	0	0	0	0
21	Croacker	0	0	0	0	0	0	0.01	0	0	0
22	Cutlassfish	0	0	0	0	0	0.01	0.004	0	0.02	0
23	Catfish	0	0	0	0	0	0	0	0	0	0
24	Weakfish	0	0	0	0	0	0	0	0	0	0
25	Cownose rays	0	0	0	0	0	0	0	0	0	0
26	Shortnose guitarfish	0	0	0	0	0	0	0	0	0	0
27	Guitarfish	0	0	0	0	0	0	0	0	0	0
28	Stingray	0	0	0	0	0	0	0	0	0	0
29	Blacktip shark	0	0	0	0	0	0	0	0	0	0
30	Dusky Shark	0	0	0	0	0	0	0	0	0	0
31	Tiger shark	0	0	0	0	0	0	0	0	0	0
32	Hammerhead sharks	0	0	0	0	0	0	0	0	0	0
33	Brazilian sharpnose shark	0	0	0	0	0	0	0	0	0	0
34	Detritus	0.55	0.7	0.2	0.37	0.7	0	0	0.235	0	0.15
	Import	0	0	0.2	0	0	0.42	0.286	0	0.29	0
	Sum	1	1	1	1	1	1	1	1	1	1

Prey/predator	12	13	14	15	16	17	18	19	20	21	22
Phytoplancton	0	0,01	0,01	0	0,59	0	0,01	0,01	0	0	0
Zooplancton	0,45	0,25	0,1	0	0,4	0,1	0	0,05	0	0	0,05
Polychaeta	0	0,1	0,1	0	0	0,35	0,15	0,15	0,05	0,12	0
Bivalves and Gastropoda	0,35	0,05	0,1	0	0	0,2	0,35	0,05	0	0,15	0
Other benthos	0,05	0,344	0,45	0,1	0,01	0,15	0,13	0,15	0,15	0,63	0,05
Shrimps	0	0,1	0,1	0	0	0,15	0,27	0,15	0,3	0,05	0
Squids	0	0	0	0,01	0	0	0	0,01	0	0	0,02
Lutjanidae	0	0	0	0	0	0	0	0	0	0	0
Swimming crabs	0	0	0,02	0	0	0,05	0,05	0,05	0,26	0	0
Mackerel	0	0	0	0	0	0	0	0	0	0	0
Reef herbivorous	0	0,03	0	0	0	0	0	0	0	0	0
Reef planctivorous	0	0	0	0	0	0	0	0	0	0	0
Reef carnivorous	0	0	0	0	0	0	0	0	0	0	0
Triggerfish	0	0	0	0	0	0	0	0	0	0	0
Blue Runner	0	0	0	0	0	0	0	0	0	0	0
Planctivorous	0	0	0	0,7	0	0	0	0,2	0	0,05	0,3
Small carnivorous	0	0	0	0	0	0	0	0,09	0	0	0
Zoobentivorous	0	0	0	0	0	0	0	0	0	0	0,15
Intermediate carnivorous	0	0	0	0	0	0	0	0	0,04	0	0,1
Large carnivorous	0	0	0	0	0	0	0	0	0	0	0,1
Croacker	0	0	0	0	0	0	0	0	0	0	0
Cutlassfish	0	0	0	0	0	0	0	0	0	0	0
Catfish	0	0	0	0	0	0	0	0	0	0	0
Weakfish	0	0	0	0	0	0	0	0	0	0	0
Cownose rays	0	0	0	0	0	0	0	0	0	0	0
Shortnose guitarfish	0	0	0	0	0	0	0	0	0	0	0
Guitarfish	0	0	0	0	0	0	0	0	0	0	0
Stingray	0	0	0	0	0	0	0	0	0	0	0
Blacktip shark	0	0	0	0	0	0	0	0	0	0	0
Dusky Shark	0	0	0	0	0	0	0	0	0	0	0
Tiger shark	0	0	0	0	0	0	0	0	0	0	0
Hammerhead sharks	0	0	0	0	0	0	0	0	0	0	0
Brazilian sharpnose shark	0	0	0	0	0	0	0	0	0	0	0
Detritus	0	0,116	0,05	0	0	0	0,04	0	0	0	0
Import	0,15	0	0,07	0,19	0	0	0	0,09	0,2	0	0,23
Sum	1	1	1	1	1	1	1	1	1	1	1

Prey/predator	23	24	25	26	27	28	29	30	31	32	33
Phytoplancton	0,01	0	0	0	0	0	0	0	0	0	0
Zooplancton	0,05	0,15	0	0	0	0	0	0	0	0	0
Polychaeta	0,2	0,1	0,1	0,35	0	0,1	0	0	0	0	0
Bivalves and Gastropoda	0,2	0,02	0,77	0	0	0,05	0	0	0	0	0
Other benthos	0,2	0,08	0	0,25	0	0,16	0	0	0,05	0	0
Shrimps	0,2	0	0,1	0,25	0,35	0,61	0,01	0,01	0,01	0,01	0,02
Squids	0	0,01	0	0	0,06	0	0,08	0,08	0,01	0,24	0,08
Lutjanidae	0	0	0	0	0	0	0	0,02	0	0	0
Swimming crabs	0,05	0	0,02	0,1	0,35	0	0	0	0	0	0
Mackerel	0	0	0	0	0	0	0	0	0	0,01	0
Reef herbivorous	0	0	0	0	0	0	0	0	0	0	0
Reef planctivorous	0	0	0	0	0	0	0,03	0,03	0,02	0	0
Reef carnivorous	0	0	0	0	0	0,01	0,08	0,05	0,1	0,01	0,05
Triggerfish	0	0	0	0	0	0	0,01	0	0,01	0,01	0
Blue Runner	0	0	0	0	0	0	0	0,02	0	0	0
Planctivorous	0,02	0,1	0	0,01	0,01	0,02	0,25	0,09	0	0,16	0,05
Small carnivorous	0	0	0,01	0	0,15	0,01	0	0	0	0	0,03
Zoobentivorous	0	0,2	0	0	0,08	0,01	0,1	0,02	0,15	0,04	0,3
Intermediate carnivorous	0	0	0	0	0	0	0,09	0,3	0,1	0,12	0,2
Large carnivorous	0	0	0	0	0	0	0,1	0,13	0,07	0,1	0,12
Croacker	0	0	0	0	0	0	0,08	0,05	0,02	0,07	0
Cutlassfish	0	0,01	0	0	0	0	0,1	0,1	0,05	0,08	0,08
Catfish	0	0	0	0	0	0,01	0	0	0	0	0
Weakfish	0	0,05	0	0	0	0	0	0	0	0,03	0,07
Cownose rays	0	0	0	0	0	0	0,01	0,05	0,01	0,05	0
Shortnose guitarfish	0	0	0	0	0	0	0	0	0	0	0
Guitarfish	0	0	0	0	0	0	0	0	0	0	0
Stingray	0	0	0	0	0	0	0,01	0,01	0,05	0,05	0
Blacktip shark	0	0	0	0	0	0	0	0	0,01	0	0
Dusky Shark	0	0	0	0	0	0	0	0	0	0	0
Tiger shark	0	0	0	0	0	0	0	0	0	0	0
Hammerhead sharks	0	0	0	0	0	0	0	0	0,01	0	0
Brazilian sharpnose shark	0	0	0	0	0	0	0	0,04	0,01	0,02	0
Detritus	0,07	0	0	0	0	0	0	0	0	0	0
Import	0	0,28	0	0,04	0	0,02	0,05	0	0,32	0	0
Sum	1	1	1	1	1	1	1	1	1	1	1

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SUPPLEMENTARY MATERIAL D – PREBAL CRITERIA

	Group name	Biomass (t/km2)	Production / consumption	Flow to detr.	Net efficiency	Respiration / assimilation	Respiration / biomass (/year)
1	Phytoplancton	24.17		2472.71			
2	Zooplancton	7.60	0.25	271.68	0.31	0.69	88.00
3	Polychaeta	3.30	0.20	256.56	0.25	0.75	213.20
4	Bivalves and Gastropoda	3.19	0.16	166.85	0.20	0.80	149.08
5	Other benthos	33.23	0.33	115.82	0.42	0.58	7.51
6	Shrimps	8.70	0.36	58.51	0.45	0.55	7.90
7	Squids	0.40	0.38	2.08	0.48	0.52	4.73
8	Lutjanidae	0.15	0.09	0.15	0.11	0.89	2.49
9	Swimming crabs	5.67	0.25	11.80	0.31	0.69	4.40
10	Mackerel	0.10	0.06	0.09	0.08	0.92	3.10
11	Reef herbivorous	1.27	0.04	8.39	0.05	0.95	20.80
12	Reef planctivorous	0.44	0.11	1.45	0.14	0.86	7.53
13	Reef carnivorous	0.28	0.12	0.57	0.15	0.85	4.50
14	Triggerfish	0.73	0.08	1.14	0.10	0.90	4.04
15	Blue Runner	0.20	0.13	0.37	0.16	0.84	4.02
16	Planctivorous	4.55	0.06	23.40	0.07	0.93	19.06
17	Small carnivorous	1.87	0.17	4.90	0.21	0.79	6.42
18	Zoobentivorous	3.18	0.14	8.56	0.17	0.83	5.91
19	Intermediate carnivorous	2.44	0.17	6.92	0.21	0.79	5.46
20	Large carnivorous	2.40	0.11	3.64	0.14	0.86	3.99
21	Croacker	0.34	0.22	0.50	0.27	0.73	2.50
22	Cutlassfish	0.20	0.16	0.14	0.20	0.80	2.17
23	Catfish	1.70	0.10	5.94	0.13	0.87	8.18
24	Weakfish	0.50	0.10	0.66	0.12	0.88	4.35
25	Cownose rays	0.12	0.07	0.12	0.08	0.92	3.01
26	Shortnose guitarfish	0.17	0.08	0.33	0.10	0.90	5.04
27	Guitarfish	0.10	0.07	0.12	0.08	0.92	3.53
28	Stingray	0.01	0.08	0.01	0.10	0.90	4.58
29	Blacktip shark	0.00	0.14	0.00	0.17	0.83	1.85

	Group name	Biomass (t/km2)	Production / consumption	Flow to detr.	Net efficiency	Respiration / assimilation	Respiration / biomass (/year)
30	Dusky Shark	0.01	0.05	0.00	0.07	0.93	1.35
31	Tiger shark	0.00	0.13	0.00	0.16	0.84	1.35
32	Hammerhead sharks	0.04	0.07	0.02	0.08	0.92	1.50
33	Brazilian sharpnose shark	0.02	0.10	0.03	0.13	0.87	3.77
34	Detritus		0.00	0.00	0.00		

SUPPLEMENTARY MATERIAL E – KEYSTONE SPECIES FULL LIST

Group name	Keystone index #1	Group name	Keystone index #2	Group name	Keystone index #3
Bivalves and Gastropoda	0.0508	Tiger shark	3.923	Hammerhead sharks	1.457
Mackerel	0.023	Dusky Shark	3.64	Mackerel	1.455
Hammerhead sharks	0.00989	Hammerhead sharks	3.432	Reef carnivorous	1.276
Intermediate carnivorous	-0.0234	Brazilian sharpnose shark	3.379	Brazilian sharpnose shark	1.103
Reef carnivorous	-0.0265	Blacktip shark	3.346	Dusky Shark	1.079
Large carnivorous	-0.0752	Mackerel	3.053	Intermediate carnivorous	0.987
Polychaeta	-0.118	Stingray	2.976	Large carnivorous	0.976
Phytoplancton	-0.133	Reef carnivorous	2.557	Bivalves and Gastropoda	0.967
Shrimps	-0.153	Squids	2.1	Squids	0.928
Other benthos	-0.178	Cutlassfish	2.052	Tiger shark	0.907
Zooplancton	-0.182	Weakfish	1.993	Weakfish	0.867
Planctivorous	-0.204	Cownose rays	1.866	Polychaeta	0.74
Squids	-0.329	Guitarfish	1.833	Cutlassfish	0.645
Weakfish	-0.339	Blue Runner	1.797	Zoobentivorous	0.611
Zoobentivorous	-0.356	Intermediate carnivorous	1.629	Planctivorous	0.593
Brazilian sharpnose shark	-0.36	Croacker	1.629	Zooplancton	0.452
Swimming crabs	-0.398	Bivalves and Gastropoda	1.59	Stingray	0.423
Dusky Shark	-0.413	Lutjanidae	1.59	Blue Runner	0.411
Tiger shark	-0.598	Large carnivorous	1.584	Small carnivorous	0.411
Small carnivorous	-0.676	Polychaeta	1.407	Croacker	0.41
Cutlassfish	-0.678	Reef planctivorous	1.256	Catfish	0.397
Catfish	-0.723	Planctivorous	1.186	Shrimps	0.361
Croacker	-0.87	Zoobentivorous	1.184	Swimming crabs	0.324
Blue Runner	-0.932	Small carnivorous	1.089	Cownose rays	0.311
Stingray	-1.054	Catfish	1.083	Phytoplancton	0.279
Cownose rays	-1.087	Shortnose guitarfish	1.037	Guitarfish	0.218
Reef planctivorous	-1.132	Zooplancton	0.999	Blacktip shark	0.19
Guitarfish	-1.197	Shrimps	0.974	Lutjanidae	0.116
Lutjanidae	-1.265	Swimming crabs	0.901	Reef planctivorous	0.1
Blacktip shark	-1.328	Triggerfish	0.654	Other benthos	-0.0163
Reef herbivorous	-1.436	Phytoplancton	0.625	Reef herbivorous	-0.284
Triggerfish	-1.515	Reef herbivorous	0.495	Triggerfish	-0.336
Shortnose guitarfish	-1.763	Other benthos	0.492	Shortnose guitarfish	-0.401